Temporal isolation of neural processes underlying face preference decisions

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Decisions about whether we like someone are often made so rapidly from first impressions that it is difficult to examine the engagement of neural structures at specific points in time. Here, we used a temporally extended decision-making paradigm to examine brain activation with functional MRI (fMRI) at sequential stages of the decision-making process. Activity in reward-related brain structures—the nucleus accumbens (NAC) and orbitofrontal cortex (OFC)—was found to occur at temporally dissociable phases while subjects decided which of two unfamiliar faces they preferred. Increases in activation in the OFC occurred late in the trial, consistent with a role for this area in computing the decision of which face to choose. Signal increases in the NAC occurred early in the trial, consistent with a role for this area in initial preference formation. Moreover, early signal increases in the NAC also occurred while subjects performed a control task (judging face roundness) when these data were analyzed on the basis of which of those faces were subsequently chosen as preferred in a later task. The findings support a model in which rapid, automatic engagement of the NAC conveys a preference signal to the OFC, which in turn is used to guide choice.

fMRI | nucleus accumbens | orbitofrontal cortex

The formation of preferences is a fundamental evaluative mechanism that precedes many other cognitive processes, such as recognition and categorization (1). Despite the ubiquity of preference decisions in everyday life, little is known about their underlying neural substrates, in part because the rapid nature of the decisions makes it difficult to uncover separate neural signals specifically attributable to the decision process with the limited temporal resolution afforded by standard hemodynamic imaging techniques, such as functional MRI (fMRI).

Here, we aimed to uncover the contributions made by specific neural mechanisms at different points in time culminating in preference-based decisions. We used faces as stimuli because these constitute a common type of stimulus about which we make preference decisions all of the time in real life. Face preference decisions appear to be causally related to basic orienting mechanisms (2) and are driven in part by universal and biologically based factors (3–5). We hypothesized that the nucleus accumbens (NAC) and orbitofrontal cortex (OFC) would both play a role but that they would be engaged during temporally dissociable epochs. These two regions are interconnected (6, 7) and have been implicated in reward-based learning (8-11) and preference decisions for a variety of stimuli (12–14). Furthermore, they are activated during assessment of affective aspects of facial stimuli, such as attractiveness (15, 16). Yet, none of these studies has been able to determine the order in time at which these structures come into play, severely limiting models of how the flow of visual information about a face ultimately results in behavioral choice.

To dissociate processes in time with fMRI, we developed a method for temporally extended decision-making (TED), in which viewers were instructed to choose a preferred face within 30 s from a pair of faces that were repeatedly presented at the center of the screen, one face alternating with the other (Fig. 1). In a control condition, subjects saw the very same faces but now

had to make a simple physical judgment as to which face looked more round. To obtain decisions that were sufficiently extended in time (i.e., sufficiently difficult that they would not be made too quickly), we preselected each pair of faces to be similar both on perceived attractiveness as well as roundness, using prior ratings obtained from a separate group of subjects.

Results

Explicit Preference Decisions. We first analyzed the preference data from 14 subjects who underwent the preference task before the control roundness task (preference-first group). The mean number of cycles of face repetitions required to make the preference choice and the mean corresponding reaction times across all trials were 1.97 ± 0.66 cycles (the modal value was two cycles) and 7.32 ± 2.73 s, respectively [supporting information (SI) Fig. 4]. Group data were analyzed by selecting only those trials from every subject consisting of two cycles of face presentation, to eliminate variability due to different numbers of faces or different decision-making times (see *Methods* for details).

Contrasts were set up between those faces eventually chosen (C) or unchosen (U) by the subject for two different points in time: the first (early) and the second (late) cycle of pairwise comparisons, thus sampling brain activity related to the same stimulus contrast at sequential points in time during the decisionmaking process. The main contrast of C–U faces within the early cycle of trials (C_E–U_E), using a random effects analysis, showed a significant effect in the right NAC [x = 15, y = 3, z = -12; Z =3.50, P < 0.001 (all P values are uncorrected in this article); Fig. 24] but no significant increases in activation anywhere in the prefrontal cortex (see SI Table 1 for complete list of regions activated). However, the contrast for the late cycle of trials (C_L-U_L) revealed significant effects in the left medial OFC (mOFC; x = -15, y = 27, z = -15; Z = 3.78, P < 0.001; Fig. 2B) and left operculum (OP)/insula (INS) (x = -39, y = 0, z = 15; Z = 3.94, P < 0.001; Fig. 2C) but no significant increases in activation in the NAC. A post hoc statistical analysis, using these three foci as regions of interest, yielded a significant region X time interaction [F(2, 26) = 6.27, P < 0.006], confirming that NAC responds more during the early compared with the late cycle, whereas mOFC and OP/INS show the converse pattern (Fig. 2D). We included the regression coefficients at the time of response (i.e., key press), to examine to what degree any of the above regions might be related to generating the actual motor

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Abbreviations: BOLD, blood oxygenation level dependent; C, chosen; fMRI, functional MRI; mOFC, medial orbitofrontal cortex; NAC, nucleus accumbens; OFC, orbitofrontal cortex; OP/INS, operculum/insula; TED, temporally extended decision-making; U, not chosen.

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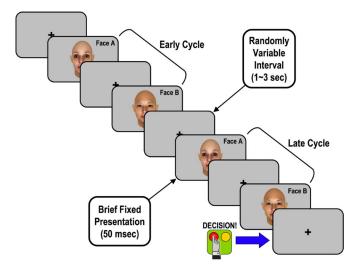


Fig. 1. Schematic diagram of a typical decision trial in the experiment. For each trial, two faces were briefly presented (50 ms) and repeated with one face alternating with the other until a subject makes a decision within 30 s by pressing a key. A blank screen with a cross-hair was inserted between each face presentation with a randomly varying interval between 1 and 3 s.

command. Of the three regions of interest (i.e., NAC, mOFC, and OP/INS), only OP/INS showed differential activity in both tasks, and the activity increases were present even at the time of key press, indicating that activity in OP/INS relates to the preparation of motor responses (SI Fig. 5).

Roundness Decision. For the roundness judgment task (C-U for roundness), we did not see any significant signal differences between chosen and unchosen faces (at P < 0.01) in either NAC or OFC, although the OP/INS was activated in the late cycle (x =-45, y = -6, z = 15; Z = 3.93, P < 0.001), once again suggesting a more general role for this region in response selection irrespective of the type of decision involved. To eliminate the possibility of a potential order effect, we ran an additional 11 subjects with the task order reversed: roundness task first, followed by preference task. In this group, we obtained data on the roundness task very similar to those described above: no significant activity in NAC or OFC but only in OP/INS (x = -42, y = 15, z = 0; Z = 3.55, P < 0.001; SI Fig. 6B). Moreover, a direct comparison between the preference task from the preferencefirst group and the roundness task from the roundness-first group confirmed that NAC and OFC are significantly more activated during preference than roundness judgments at P <0.005, indicating no significant contribution of task order to the increases in activation we saw in NAC and OFC (see SI Fig. 7). Eye-tracking data collected from additional subjects also confirmed that the differential activations we found could not have resulted simply from different patterns of gaze fixation in the two decision tasks (see SI Fig. 8).

Effect of Novelty. We next examined data from the additional 11 subjects who performed the preference task on faces that they had already seen during the roundness task in their first run (roundness-first group). Intriguingly, activity for the contrast (C–U) in the preference task was no longer present in the NAC at either early or late cycles. The response in OFC was still present at the late cycle, as it had been for the preference-first group (x = -15, y = 36, z = -18; Z = 2.96, P < 0.005; SI Fig. 6.4). These results suggest that preference-specific signals in NAC, but not mOFC, are influenced by stimulus novelty. As further evidence of this, we undertook an analysis of preference trials that consisted of only a single cycle (as opposed to the

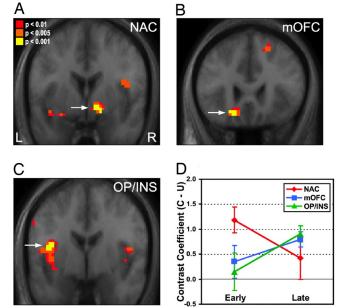


Fig. 2. Regions showing greater response to chosen (C) vs. unchosen (U) faces in the preference-first group at different time points while deciding which face was preferred. (A) A statistical contrast map at the early repetition of faces (CE-UE) showing right NAC (arrow; x=15, y=3, z=-12; Z=3.50, P<0.001, uncorrected). (B and C) Statistical contrast maps of C-U for the late repetition of two cycle trials (CL-UL) shows left mOFC (x=-15, y=27, z=-15; Z=3.78, Z=3.7

two-cycle trials on which all other analyses in this article are based). Here, we found increases in activation in bilateral NAC, but not in mOFC (SI Fig. 9; see also SI Fig. 10 for analysis on the trials with three cycles).

Implicit Preference in the NAC. NAC was activated only during early, but not late, cycles and only to novel faces, which led us to hypothesize that it might extract first impressions from faces automatically and implicitly. To test this hypothesis, we analyzed the blood oxygenation level-dependent (BOLD) signal to faces during the roundness task in the roundness-first group according to each subject's subsequent decision on the forthcoming preference task (see Fig. 3A). That is, chosen and unchosen faces were labeled not on the basis of the roundness decision (even though the BOLD responses were measured during the roundness task), but rather on the basis of the preference task, which took place some time later. Because the face stimuli used in the two tasks were identical, we could examine activation that might be driven by the perceived preference of a face even though all of the subjects reported in debriefing that they were not consciously aware of preference-related judgments on the faces during their roundness decision task. Interestingly, this analysis of data from the roundness task based on implicit preferences revealed significant effects in the NAC at the first cycle of faces, just as we had found during explicit preference decisions in the preference-first group (x = 12, y = 3, z = -15; Z = 3.59, P <0.001; Fig. 3B). An analogous analysis of data from the roundness task, based on preference judgments made in a separate session, but this time in the subjects who performed roundness decisions after preference decisions, revealed that mOFC, rather than NAC, was more active after presentation of a face that had been designated as preferred compared with that which had been designated as unpreferred (Fig. 3C). NAC responses to preferred

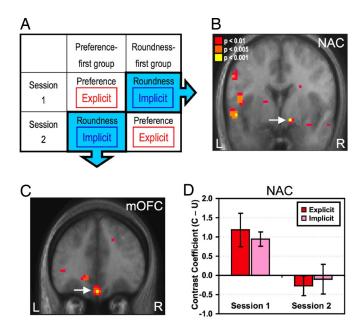


Fig. 3. Brain responses to implicit face preferences. (*A*) Overall order of tasks in the two subject groups. The labels "Explicit" and "Implicit" refer to the kind of preference judgments in each task. While subjects performed an explicit roundness decision, we contrasted faces based on subjects' choices to those same faces in the preference decision task performed either earlier or later to examine neural activities related to implicit preference (shown in *B* and *O*. (*B*) NAC activity (arrows; x = 12, y = 3, z = -15; Z = 3.59, P < 0.001) in early cycles during roundness judgments correlating with subsequent preference judgments in the roundness-first group. (*C*) Implicit preference during the roundness task from the preference-first group showed a significant correlation with the activity in mOFC (x = 0, y = 39, z = -27; z = 3.06, P = 0.001) at early cycles. (*D*) NAC showing greater responses to preferred vs. nonpreferred faces during early cycles for first, but not second, decisions on the same faces, regardless of the decision task that was explicitly performed.

vs. nonpreferred faces during early cycles were significantly greater in first than second decisions (i.e., sessions) on the same faces in both implicit [t(23) = 2.22, P < 0.05] and explicit [t(22) = 3.07, P < 0.05] preference tasks, suggesting specific engagement of NAC in face preference judgments only at the first presentation, regardless of attentional focus (Fig. 3D).

Individual vs. Group Preference Decisions. Analysis of the preference decisions from all of the subjects who participated in the fMRI experiments plus an additional 12 subjects from a separate behavioral study (a total of 37 subjects) revealed 74.5% agreement on average across subjects in their preference decisions, significantly greater than chance [t(36) = 10.98, P < 0.001],although individual differences were present as well. It would be of interest to investigate whether the consensus group judgments, as opposed to individual subjects' idiosyncratic judgments, are driving the NAC activation that we observed. To investigate this issue, we included both mean group preference decisions (from all of the 37 subjects) and each subject's individual preference as regressors in our analysis, to examine separately their contribution to NAC activation. We found that NAC activation correlated significantly with group rather than individual preference decisions (x = 12, y = 15, z = -3; Z = 2.98, P < 0.005; SI Fig. 11A) during early cycles, whereas mOFC activity significantly correlated with individual rather than group preference decisions (x = 18, y = 27, z = -15; Z = 3.61, P < 0.0000.001; SI Fig. 11B) during late cycles.

Effect of Absolute Level of Facial Attractiveness on NAC Activity. We showed that BOLD response in the NAC reflects preferences for

faces even in the absence of an explicit judgment or choice that would reveal those preferences at the time. This raises the possibility that response in the NAC might be driven by the absolute attractiveness of a face, rather than its relative preference (because, on average, the set of all of the preferred faces would have greater absolute attractiveness than the set of all of the unpreferred faces). Thus, we ran additional analyses to test the contribution of facial attractiveness, as measured from their normative ratings, to the BOLD response seen in the NAC during face preference decisions. Again restricting ourselves to the data from the two-cycle trials, we grouped both chosen and unchosen face events separately for early and late cycles, with two parametric modulators: preference choices and attractiveness ratings. A significant correlation with preference choices was observed again in right NAC (x = 9, y = 6, z = -9; Z = 3.63,P < 0.001; SI Fig. 124), even after excluding BOLD signal variances explained by facial attractiveness. Significant correlations with attractiveness ratings were found in the bilateral middle temporal gyri (x = 63, y = -36, z = -18; Z = 3.70, P < 0.0000.001; x = 63, y = -33, z = -21; Z = 3.34, P < 0.001; SI Fig. 12B) but not in NAC. These findings confirm that BOLD response in the NAC contributes to decisions by forming implicit preferences for one face over another rather than merely responding to absolute facial attractiveness (or to the physical features that make faces attractive as such).

Discussion

In the present study, we used a temporally extended decision-making task to dissociate the roles of specific neural structures at different points in time during face preference decision-making, using fMRI. We found that two regions in particular, the NAC and the mOFC, are involved in face preference decisions and that these structures contribute at different times during the decision process. NAC was activated early on, when subjects were presented with the two faces for the first time, whereas mOFC was engaged later, at the point when subjects made their decision as to which face they preferred.

NAC and OFC are two major subcortical and cortical brain structures, respectively, that have been strongly implicated in reward-related processing in both animals and humans (9, 10, 17). There has been much interest in differentiating the functional contributions made by these two structures, and a number of putative functional dissociations have been proposed. For instance, it has been suggested that the ventral striatum is involved in encoding errors in prediction for future rewards, whereas the OFC contributes to encoding of stimulus-reward value and in representing expected future rewards (8). Another hypothesis is that ventral striatum plays a role in reward anticipation, whereas medial prefrontal cortex is involved in responding to receipt of the outcome itself (18). The present study provides new insights into the putative distinct contributions of these two structures by suggesting that these areas are engaged at distinct times during the decision process. NAC showed differential responses to preferred faces only on the first cycle of face presentations, and even then only when the faces were presented for the first time. This effect cannot be attributed to a simple novelty effect alone because the effect was specific to the contrasts made between preferred vs. nonpreferred faces. Rather, our results are compatible with the suggestion that NAC is involved in forming an initial affective evaluation of the faces, a process perhaps akin to how we form first impressions of others in everyday life.

It is notable that activity in NAC during the first cycle discriminated between preferred and nonpreferred faces even when subjects were performing an unrelated roundness judgment task and were not explicitly making preference judgments. This was the case for subjects who underwent the roundness judgment task first and only subsequently were asked to judge

the faces in terms of preference. When neural activity during the roundness trials was analyzed according to subjects' subsequent preferences in the later preference task, we still found increased activity in NAC to faces that would subsequently be preferred compared with faces that would not be preferred. Interestingly, in those subjects who underwent the preference task first, activity in NAC was not present during the subsequent roundness task. These results suggest that NAC may be specifically involved in forming initial preference judgments on the faces and that such judgments may be engaged automatically even without explicitly requiring subjects to make preference judgments. Moreover, we did not find significant correlations between NAC activity and normative ratings of attractiveness, which argues against a less specific role for NAC in facial attractiveness per se. Rather, our findings suggest that this region contributes specifically to preference formation, perhaps under situations where multiple stimuli need to be evaluated for their relative preferences. Once the initial preferences are formed, then NAC no longer discriminates between preferred and nonpreferred faces either during the decision trial itself or even during subsequent trials in which the same face pairs are presented.

By contrast with the NAC, mOFC showed preference-related activation only during the late cycle of preference decisions, irrespective of whether this was the first time the faces were presented or whether the face pair had already been seen. Furthermore, in those subjects who made preference decisions in the first run, activity in mOFC was also present during the second run, while subjects made roundness decisions. In this case, however, activity increased in mOFC when subjects were presented with the face that was categorized as being preferred during the preference task. These results suggest that mOFC may be more involved in encoding already formed preferences (which are initially mediated by the NAC). Moreover, once a preference judgment has been rendered, after a subsequent presentation of the same faces, mOFC once again discriminates between which face is preferred and which is not, suggesting that this region is also involved in reprising formed preference judgments, perhaps by retrieving these representations from memory. Taken together, these results are compatible with the suggestion that mOFC plays a key role in holding representations of previously formed preferences on-line, so that these representations can be used to guide subsequent behavioral choice (12, 19).

It is noteworthy that BOLD responses within the NAC were better correlated with preference judgments averaged across the entire group of subjects than with individual judgments, whereas BOLD responses within the mOFC were better correlated with the preference judgments provided by each individual subject than with group judgments. The differential nature of this effect would seem to rule out a simple effect of statistical power—i.e., that individual ratings were simply noisier than the group ratings. Rather, we suggest that NAC activity reflects a relatively automatic and rapid preference process that is shared in common across subjects, whereas OFC responses subserve a more idiosyncratic and flexible judgment on which final explicit decisions can be based. This interpretation would also be consistent with dual process theories in which an automatic and implicit evaluation of an object can be overridden by (or sometimes coexist with) a deliberate and explicit evaluation of the same object (20, 21).

Face preference decisions, such as those being studied in the present experiment, will ultimately be driven by features of the face that underlie factors, attractiveness and emotional expression, and by the degree of familiarity to the subject. Because we made an effort to use face pairs that were highly similar, the role of the absolute values of these factors in our experiment is likely to be small, as borne out by the finding that absolute facial attractiveness did not contribute to NAC activity during face preference decisions (SI Fig. 12). Despite this, subjects' preference choices were also quite reliable (SI Fig. 13), and an important direction for future research will be to determine the extent to which these different putative factors contribute to the preference decision-making process and to the underlying neural substrates that we have identified here. The temporally extended decision-making paradigm that we have developed here could also be used in future studies to probe the neural underpinnings of other more complex social judgments.

Our findings provide evidence that during an elementary form of decision-making—preference formation on the basis of visual features of a face alone—neural structures implicated in reward and reward-based decision-making, such as the NAC and OFC, are strongly engaged in humans. The observed temporal dissociation between NAC and OFC is consistent with the suggestion that subcortical and cortical systems play at least partly dissociable roles in emotional processing (22, 23). Finally, our findings resonate with dual process theories from social psychology and decision science, whereby an initial rapid, automatic, but often less accurate evaluative system is proposed to exist either cooperatively or competitively alongside a slower, but often more accurate, deliberative system. It is tempting to speculate on the basis of the present results that the distinct contributions of NAC and mOFC found here may map onto these proposed theoretical distinctions (24, 25).

Methods

Subjects. Twenty-eight right-handed healthy normal subjects participated in the fMRI experiment. Given that the main purpose of our study was to examine the temporal dynamics of decision-making, it was necessary to obtain enough trials with long reaction times. Therefore, three subjects were excluded from the analysis because those subjects lacked trials with more than one cycle of face repetitions. All of the subjects performed both preference and roundness decision tasks on computergenerated faces; 14 subjects (7 males; mean age = 22.79 ± 2.55 , age range = 20-27) performed the preference decision task first (preference-first group), and 11 subjects performed the roundness decision task first (roundness-first group) (6 males; mean age = 26.55 ± 7.06 , age range = 18-45). All subjects gave informed consent, and the study was approved by the Institutional Review Board of the California Institute of Technology.

Stimuli and Task. Stimuli were presented through MRI-compatible goggles (Resonance Technology), and subjects made choices with an MRI-compatible button box. We constructed 40 pairs of faces from 80 different faces generated with the same computer software (FaceGen; Singular Inversions) that was used in a prior study of ours (2). To make decisions relatively difficult and lead to a high proportion of two-cycle trials, the two faces in each pair were approximately equated in terms of attractiveness, and roundness ratings on the basis of data collected in a pilot study and the same face pairs have been used for all of the subjects in the present study. On each trial, each face was briefly presented (50 ms) and repeatedly alternated with the second face. An interstimulus interval randomly varying between 1 and 3 s consisted of a blank screen with a central cross-hair and followed each face presentation (Fig. 1), to achieve separation between overlapping hemodynamic responses to the two face stimuli (26). A pilot behavioral study indicated that this temporal scheme provided sufficient trials with long decision times. Although subjects were required to make their decision within 30 s, all took considerably less time than this (SI Fig. 4), indicating that the preference decision was made spontaneously. Before the experiment, subjects performed several practice trials that consisted of two colored squares instead of face images and were asked to choose a more bluish square. In addition to the preference decision task, subjects also underwent a roundness judgment task, during which they were presented with the same faces in the same temporally extended paradigm, but instead of judging preference had to make a simple physical judgment as to which face looked more round. The instructions for both tasks were: "Choose a PREFERRED face: Who would you like to approach and talk to?"

for preference decision task and "Choose a ROUNDER face: Which face is rounder than the other?" for roundness decision task. Subjects were required to make decisions by pressing one of two buttons with their right hands according to a text cue located either at left-bottom corner ("Left") or at right-bottom corner ("Right"). Every trial started with a face with left cue, to minimize subjects' attention toward the cues. The order of presentation of these tasks was approximately counterbalanced across subjects, with 14 subjects undergoing the preference task first and 11 subjects undergoing the roundness task first.

Imaging Procedures. The functional imaging was conducted on a 3 tesla Siemens TRIO MRI scanner. For each subject, we acquired whole-brain T1-weighted anatomical scans (2,565,256 voxels; 15,151-mm in-plane resolution; 176 axial slices) and gradient echo T2*-weighted echo planar images (EPI) with BOLD contrast (64,564 voxels; repetition time = 2,000 ms; echo time = 30 ms; 35,353-mm in-plane resolution; 32 oblique axial slices). We used a tilted acquisition sequence at 30° to the AC-PC line to recover signal loss in mOFC (27). In addition, we used an eight-channel phased array coil that yields a ≈40% signal increase in mOFC over a standard head coil. Visual inspection of raw echo planar images showed excellent signal quality in the mOFC. Each brain volume comprised 32 axial slices of 3-mm thickness and 3-mm in-plane resolution. Each scan lasted ≈10 min depending on performance, and the first five volumes of images were discarded to allow for equilibration effects.

Imaging Data Analysis. Image analysis was performed by using SPM2 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, U.K.). To correct for subject motion, the images were realigned to the first volume and spatially normalized to a standard T2* template with a resampled voxel size of 3 mm³, and spatial smoothing was applied by using a Gaussian kernel with a full width at FWHM of 8 mm.

All of the trials were sorted by the number of cycles of face repetitions required to make decisions, and all of the events of face presentation were categorized into chosen and unchosen faces, based on subjects' decisions. For data analysis, we selected only those trials with two cycles from each subject, because (i) all of the final subjects had such trials, (ii) these were overall the most frequent trials, and (iii) two cycles provide the simplest initial approach to examining discrete temporal epochs in decisionmaking. Thus, although all subjects made their decisions spontaneously and without the effect of a time limit, we selected a subset of the data such that all subjects nonetheless saw an equal number of face exposures to arrive at their decision. The onset times of face presentation events were sorted by the cycle length (i.e., the number of cycles repeated), the decision (i.e., chosen or unchosen), and the cycle of presentation [i.e., first (early) and second (late) cycle time-locked to the time of button press and then convolved with a canonical hemodynamic response function and entered into a regression analysis against the fMRI data.

We ran three additional separate analyses. The first examined covert preference decisions during the roundness decision task, by categorizing the face presentation events based on each subject's choices on the same pairs of faces in their preference decision task (Fig. 3). The second examined brain responses involved in consen-

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sus vs. individual preference decisions, by including an additional regressor in the SPM design-matrix of consensus preference decisions obtained from all of the subjects (see SI Fig. 13). The third examined whether task modulated one of our key findings, that NAC was more activated early for those faces that were preferred. We analyzed the three-way interaction between cycle (early or late), face preference (chosen or unchosen on the preference task), and task (explicit preference judgment or explicit roundness judgment) (see SI Fig. 14). In all of the analyses, a separate regressor was created for the event of pressing the button, to isolate neural activity unique to the actual motor response, and the six scan-to-scan motion parameters produced during realignment were included to account for residual effects of movement.

Linear contrasts of regressor coefficients were computed at the individual subject level to enable comparisons between chosen and unchosen faces separately for different lengths of trials. The results from each subject were taken to a random effects level by including the contrast images from each single subject into a paired t test. A statistical threshold at P < 0.001 (uncorrected) was used to detect any significant signal difference in the regions of interest including the OFC, the INS, the NAC, and the amygdala, which are well known to be involved in linking emotional value of stimuli to decision-making or choice behavior (8, 10, 12, 28). To plot effects for each phase of the decision process, we extracted normalized regressor coefficients from the peak voxel of the cluster found in the statistical contrast maps of C-U at different cycles. Finally, the structural T1 images were coregistered to the mean functional echo planar images for each subject and normalized by using the parameters derived from the echo planar images. Anatomical localization was carried out by overlaying the t-maps on a normalized structural image averaged across subjects, and with reference to an anatomical atlas.

Behavioral Data from 12 Additional Subjects. We ran an additional 12 subjects to test reliability of TED decisions, validity of TED decisions based on free-viewing decisions, contribution of facial attractiveness to TED preference decisions, and potential gaze fixation difference between different conditions. We collected eye-tracking data, using a head-mounted eye tracker system (Arrington Research, Scottsdale, AZ), and the data were analyzed with MATLAB. In this experiment, a subject viewed stimuli presented on an LCD monitor and responded by using a keyboard. The same face stimuli and TED paradigm used in the original fMRI experiment were used, and two decision tasks were repeated immediately after the first tasks (i.e., R-P-R-P or P-R-P-R). After the TED tasks, subjects were asked to make decisions on the same face pairs, which were presented simultaneously on the display with free-viewing time. The free-viewing decision tasks were also followed by attractiveness and roundness rating decisions on a nine-point scale (e.g., 1, not attractive at all; 9, very attractive).

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